ECOLOGY OF *ARCTOMECON CALIFORNICA* AND *A. MERRIAMII* (PAPAVERACEAE) IN THE MOJAVE DESERT

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Abstract

Arctomecon (Papaveraceae) is composed of three rare gypsophilous species in the northeastern Mojave Desert. In order to effectively manage the remaining populations of these rare plants, which are increasingly being impacted by anthropogenic disturbance, the life history attributes, reproductive biology, vegetative associates and edaphic requirements were investigated for two species in southern Nevada: *Arctomecon californica* and *A. merriamii*. Loss of reproductive potential was highest for both species at the bud and capsule stages, and highest post-reproductive mortality occurred during the seedling stage. *Arctomecon californica* was reproductively self-incompatible, while *A. merriamii* was able to self-pollinate as well as outcross. Both species occurred in vegetation types that were quantitatively distinct and therefore unique relative to typical Mojave Desert plant assemblages. *Arctomecon* also occurred on gypsum-derived soils that were different from off-site locations, most notably in sulfur and calcium contents. Hypotheses as to why *Arctomecon* can establish on gypsum soil, and what role this soil requirement plays in the rarity of this taxa, are considered in light of these results. Habitat specificity, especially for *A. californica*, leads to the conclusion that gypsum outcrops must be preserved in order to ensure the survival of *Arctomecon* species in the Mojave Desert.

Introduction

The Endangered Species Act of 1973 has led to increased attention to species that are potentially threatened with extinction. The scientific literature is beginning to address this issue with population-level studies on rare plants (Menges and Gawler 1986; Fiedler 1987; Freas and Murphy 1988; Mehrhoff 1989). Data collection on life history parameters is necessary in order to manage species properly (Harper 1979; Owen and Rosentreter 1992), which can also serve to answer ecological and evolutionary questions (Meagher et al. 1978). Although the demographics of some species have been investigated, many rare plant species have no available demographic or functional data. Studies have shown that rare plants are often restricted to certain habitats (Menges 1990) or to a specific soil type (Nelson and Harper 1991); this endemism can contribute to extreme population fluctuations, which can lead to extinction of local populations or entire species (Kruckeberg and Rabinowitz 1985).

One such group of plants is the genus *Arctomecon* (Papavera-

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ceae), which consists of three rare perennial species that inhabit gypsum soils in the Mojave Desert (Meyer 1986). *Arctomecon californica* Torr. and Frem., the golden bear-claw poppy, is found in northern Arizona and southern Nevada on gypsiferous soils. It is listed by the state of Nevada as Critically Endangered, and by the Federal Government as a Category 2 candidate species (Morefield and Knight 1992). *Arctomecon merriamii* Cov., the white bear-claw poppy, occurs in both California and Nevada (Janish 1977), and is also listed by the Federal Government as a Category 2 candidate species (Morefield and Knight 1992). A third species, *A. humilis,* the dwarf bear-claw poppy, is located only in Washington County, Utah, and is federally listed as an Endangered Species. Its gypsum habitat is in danger of destruction by the growth of the city of St. George as well as off-road vehicle use (Nelson and Harper 1991).

Research on the population ecology of *A. humilis* has been conducted (Nelson and Harper 1991), but comparable studies for the other two species of *Arctomecon* have not been published. The goals of this research were to obtain an understanding of the life history and reproductive ecology of *A. californica* and *A. merriamii* in their native habitats, and to describe the vegetation and soils for sites that contain populations of each species. The interaction of these components undoubtedly play an important role in the success of *Arctomecon* species in their respective habitats. As a result, this information is critically needed in order to successfully manage each species to prevent them from federal listing and thus the threat of becoming extinct in all or part of their geographical range.

Methods

Study Sites

Studies of the two *Arctomecon* species were conducted at several locations in the Mojave Desert, a region that receives only 10–15 cm of precipitation per year, most of which occurs in the winter months. Temperature extremes range from −5°C to 49°C, so both freezing and heat stresses can be important determinants of the distribution of perennial plants in the region.

Three study sites were selected for *Arctomecon californica* within Lake Mead National Recreation Area: (1) near Overton Beach, Clark County, Nevada (36°25′N, 114°25′W, 433 m elev.), 97 km NE of Las Vegas; (2) near Stewart Point, Clark County, Nevada (36°22′N, 114°24′W, 396 m elev.), 90 km east of Las Vegas; and (3) near Temple Bar, Mohave County, Arizona (36°05′N, 114°25′W, 430 m elev.), 161 km southeast of Las Vegas.

Arctomecon merriamii was studied at Ash Meadows National Wildlife Refuge in Nye County, Nevada (36°25′N, 116°20′W, 610 m elev.), located 161 km northwest of Las Vegas. This area is under the protection of the United States Fish and Wildlife Service.

Population Structure, Life History, and Reproductive Ecology

Arctomecon species are herbaceous perennials that form basal rosettes with deep taproots. In their first year, they grow strictly vegetatively and will flower in the second year if there is adequate rainfall. After initial flowering and seed set, they can live several more years and have multiple flowering events. They also tend to form clonal plants with multiple rosettes as they age.

Individuals in each population were mapped using four 10 m^2 (1 × 10 m) transects that were placed in a systematic random fashion through the habitat. Plants were not individually mapped except for seedlings, which were marked with colored toothpicks and mapped using individual coordinates within a grid (Lesica 1987). Demographic data on each population were collected monthly from May 1992 to September 1993. The diameter of the basal rosette of each plant in the transects was obtained once every three months, increasing to once every two weeks during the flowering season. During flowering, the number of buds, flowers, and capsules were counted for each marked plant, and a sample of capsules was collected to determine the number of seeds per capsule. Comparisons of flowering parameters between sites and age classes within sites were made using a non-parametric Kruskal-Wallis H-test (SAS statistical software).

Mature plants were tested for the ability to self-pollinate by bagging individual buds with a lightweight, draw-string nylon material to prevent insect pollination. Controls were established as buds on the same plant that were marked with string but were not prevented from cross-pollinating. Both control and experimental buds were collected when mature and measured for viable seed set. Results were compared using t-tests, and are reported for *A. californica* from the Overton Beach study site only.

Vegetation and Soils

Data for vegetation analysis were collected on sites where *Arctomecon* was found, and at adjacent off-site areas where no poppies were found. Density, frequency, and cover data for *A. californica* were collected using a minimum of 30 randomly placed 1 m^2 (1 × 1 m) quadrats. Due to the extremely limited distribution of *A. merriamii*, circular plots ranging in size from 1 to 4 m radius (3–50 m^2) were used.

Percent Similarity indices were calculated for on- and off-site locations at each major site using species composition data. Percent Similarity between on- and off-site locations was calculated as

$$\text{Percent Similarity} = 1.0 - 0.5\ (\Sigma\ p_a - p_b) = \Sigma\ \min\ (p_a \text{ or } p_b)$$

where p_a was the decimal Importance Value (0 to 1) for each given species in sample A (i.e., on-site) and p_b was the decimal importance for the same species in sample B (i.e., off-site) (Whittaker 1975). The Coefficient of Community was also calculated between sites, as determined by

$$\text{Coefficient of Community} = 2S_{ab}\ /\ (S_a + S_b)$$

where S_a and S_b were the number of species in samples A and B, respectively, and S_{ab} was the number of species found in both samples (Whittaker 1975).

Soils were collected on each site with a soil corer in a random grid pattern (N = 7 for *A. californica*, N = 5 for *A. merriamii*). Soils were collected for *A. californica* from on- and off-site locations, as well as from sites that appeared similar in texture and color to the on-site location (i.e., visually appeared to be a similar gypsum outcrop) but where no *Arctomecon* were present. [Gypsum outcrops that contain *Arctomecon* populations tend to have a "badlands" appearance in which the soils are whitish in color, fluffy in texture, and tend to form raised crusts that are easily disturbed; off-site locations tend to be flat, compacted, stony surfaces that are often covered with a cemented desert pavement.] Soil cores were separated in the field into surface 0–5 cm depth and 6–15 cm depth increments, stored in separate sealed soil tins, and were immediately transported back to the laboratory. The same methodology was used for *A. merriamii*, but visually similar soils without *Arctomecon* present were not sampled. Soils were analyzed by A & L Western Agricultural Laboratories (Modesto, CA) for pH, percent organic matter, cation exchange capacity, soluble salts, total phosphorous, potassium, magnesium, calcium, sodium, sulfur, and zinc, and percent base saturation of potassium, magnesium, calcium, hydrogen, and sodium. Major components of the soil were compared between sites with Pearson product-moment correlation coefficients using Mystat statistical software.

Results

Life History and Reproductive Ecology

Data collected for both *Arctomecon californica* and *A. merriamii* were divided into size classes based on logical divisions of the plant rosette diameter, probable age, and percent flowering per size class (Table 1; ages provided are approximate, particularly the 1- and 2-yr-old plants, whereas seedlings and juveniles were accurately determined).

Overall survivorship of *A. californica* over the length of the study

TABLE 1. SIZE CLASS DESCRIPTIONS FOR *ARCTOMECON CALIFORNICA* POPULATIONS AT THREE STUDY SITES (OVERTON BEACH (OB), STEWART POINT (SP), AND TEMPLE BAR (TB)), AND FOR *A. MERRIAMII* AT ASH MEADOWS (AM).

			% flowering			
			A. californica			*A. merriamii*
Size class	Rosette diameter (cm)	Estimated age	OB	SP	TB	AM
1	0.0–0.9	Seedling	0	0	0	0
2	1.0–4.9	1 yr juvenile	0	0	0	0
3	5.0–7.4	1–2 yr juvenile	0	0	0	0
4	7.5–11.4	2–2+ yrs	73	100	100	83
5	11.5–20.9	2–2+ yrs	100	100	100	100
6	21.0–44.0	2+ yrs	100	100	100	100

(May 1992 to July 1993) was very low for all three sites, ranging from a minimum of 14% at Stewarts Point to a high of 38% at Temple Bar (Table 2). *Arctomecon merriamii,* on the other hand, showed over a four-fold increase in the number of plants from May 1992 to May 1993. Populations fluctuated widely for both species (Table 2), with *A. californica* showing a pronounced change in population numbers at the Stewart Point site. However, no such change was observed at the other two sites. There were over 300 *A. californica* recruits in 1993, but most died during the hot, dry summer months of June through August. *Arctomecon merriamii* showed a gradual decline in numbers after peak recruitment in April.

Mortality in each size class indicated that the smallest plants had the highest annual mortality (Fig. 1); seedlings (size class 1) exhibited 60–87% mortality for *A. californica* and 39% for *A. merriamii*. For *A. californica*, mortality in the larger size classes differed between the three sites. Size-specific mortality for *A. californica* was approximately 60% for seedlings at Overton Beach and Temple Bar

TABLE 2. DENSITY (PLANTS M^{-2}) OF *ARCTOMECON CALIFORNICA* AT THREE SITES AND *ARCTOMECON MERRIAMII* AT ONE SITE FROM MAY 1992 TO JULY 1993. Site abbreviations are Overton Beach (OB), Stewart Point (SP) and Temple Bar (TB) for *A. californica* and Ash Meadows (AM) for *A. merriamii.*

		A. californica			*A. merriamii*
Year	Month	OB	SP	TB	AM
1992	May	8.2	12.4	7.1	1.5
	December	1.6	8.2	3.3	1.4
1993	February	1.5	8.0	3.3	1.3
	March	2.2	18.2	3.8	5.8
	April	2.4	31.6	4.0	7.7
	May	2.2	23.1	2.7	6.5
	July	1.5	1.8	2.7	4.4

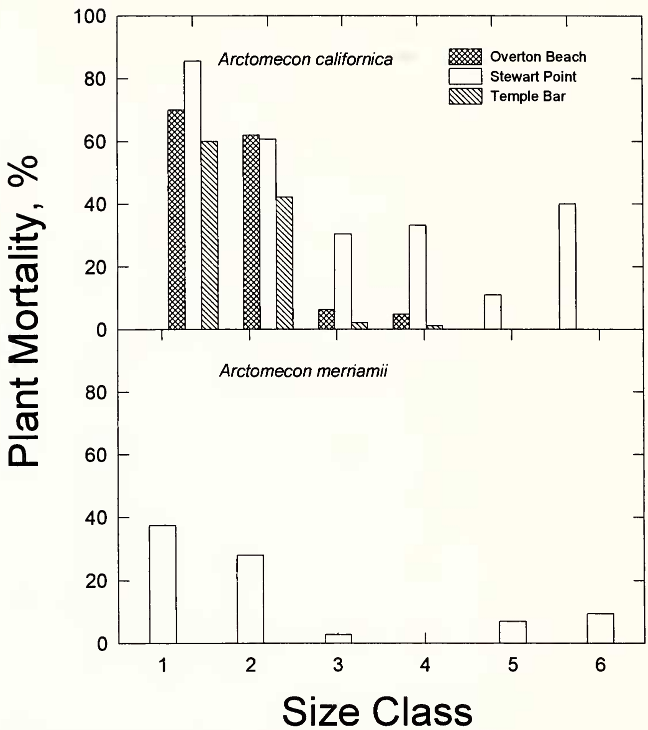

FIG. 1. Percent plant mortality for *Arctomecon california* (top) and *A. merriamii* (bottom), by size class (see Table 1), from May 1992 to September 1993.

and 80% at Stewart Point. These site differences were also consistent at the larger size classes, as *A. californica* populations at Overton Beach and Temple Bar had very low mortality rates (<5%) in size classes 3 through 6, whereas average mortality of *A. californica* populations at Stewart Point averaged about 25% in these larger size classes (Fig. 1).

Reproductive attrition is defined as the number of buds, flowers and capsules which did not produce seed on each individual plant (i.e., lost reproductive potential). This loss, by size class, showed that *A. californica* lost between 10% and 50% of its reproductive potential across all sites and size classes 3 through 6, and *A. merriamii* exhibited a 2% to 26% reproductive attrition for size classes 4 through 6 (Fig. 2). However, there were no statistically significant differences in reproductive attrition between size classes for *A. californica* ($P = 0.068$) or for *A. merriamii* ($P = 0.234$). In *A. californica*, the Stewart Point populations had the highest reproductive attrition at the largest size classes (35–45% at Stewart Point versus 10–25% at the other two sites).

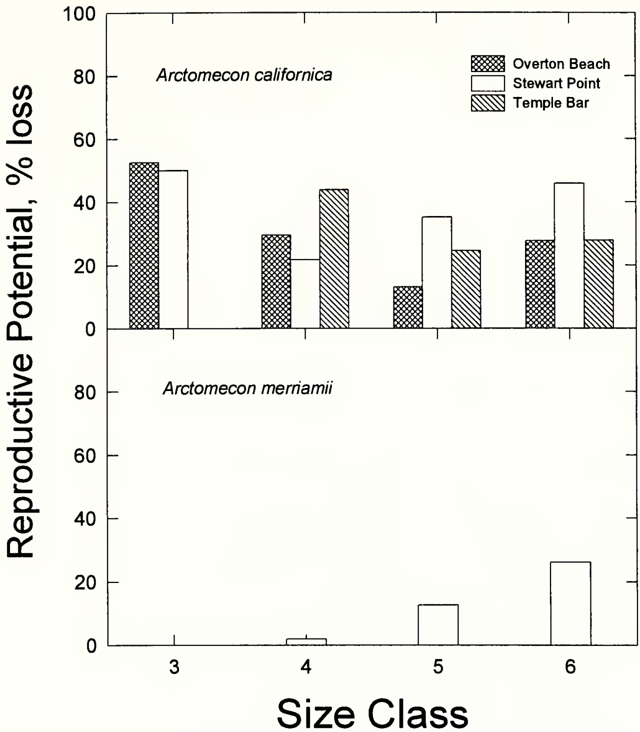

FIG. 2. Reproductive attrition (% reproductive potential lost), by size class (see Table 1), for *Arctomecon californica* (top) and *A. merriamii* (bottom) in 1993. Note: In size class 3, there was no flowering for *A. californica* at Temple Bar or for *A. merriamii.*

Reproductive attrition by reproductive stage showed a clear trend, with lower reproductive losses during flowering than at the bud and capsule stages (Table 3). This was true for *A. californica* at all three sites and for *A. merriamii*. Reproductive losses for *A. californica*

TABLE 3. REPRODUCTIVE LOSS, BY REPRODUCTIVE STAGE, FOR *ARCTOMECON CALIFORNICA* AND *A. MERRIAMII* IN 1993. Sample sizes were N = 15 (Overton Beach), N = 19 (Stewart Point), and N = 31 (Temple Bar) for *A. californica* and N = 23 for *A. merriamii.*

		Reproductive stage		
Species	Site	Bud	Flower	Capsule
A. californica	Overton Beach	15.0	3.5	12.3
	Stewart Point	22.7	0.4	12.6
	Temple Bar	24.5	1.6	2.4
A. merriamii		6.9	0.2	5.6

were 0 to 3% at the flower stage, 15 to 25% at the bud stage, and 2 to 13% at the capsule stage. There was a significant difference in the percentage lost at each site in each stage (P = 0.001 at Overton Beach, P = 0.0001 at Stewart Point and Temple Bar). A small proportion of the reproductive attrition for *A. californica*, 0.3% of the aborted buds and 5.3% of the aborted capsules, was due to herbivory by insects. Reproductive loss for *A. merriamii* also showed largest losses at the bud (6.9%) and capsule (5.6%) stages; flower abortion was very small (0.25%). However, these stage differences were not statistically significant (P = 0.058). About 15% of the aborted capsules of *A. merriamii* were due to herbivory by insects, although none of the buds were lost to herbivory.

Self-compatibility tests showed that bagged *A. californica* buds produced a lower number of seeds (3.5 ± 14) than did unbagged controls (39 ± 34; P = 0.001). Bagged buds also had a higher number of aborted seeds (89 ± 24) than did the unbagged controls (53 ± 27; P = 0.0002). Similar experiments with *A. merriamii* were less conclusive, as bagged buds had slightly, but not significantly, lower seed set (238 ± 60) than did unbagged controls (283 ± 133; P = 0.52). There was no significant difference (P = 0.46) in the number of aborted seeds between bagged buds (35 ± 22) and unbagged controls (67 ± 64).

Vegetation and Soils

Perennial species sampled in areas where *Arctomecon* populations were found (on-site) and in adjacent areas without *A. californica* (off-site) are shown in Tables 4 and 5. *Arctomecon californica* had the highest Importance Value (IV) on-site, except at Temple Bar, where it was second in IV to *Eriogonum inflatum*, an herbaceous perennial that preferentially occupies disturbed habitats (Table 4). In contrast, *A. merriamii* shared co-dominance with the C_4 halophytic shrub *Atriplex confertifolia* (shadscale) on both sites sampled. Off-site vegetation in the vicinity of *A. californica* populations was dominated by *Ambrosia dumosa* (bur-sage) and perennial grasses at Overton Beach, by *Eriogonum inflatum* at Stewart Point, and by *Larrea tridentata* (creosotebush) and assorted small perennials at Temple Bar (Table 4). In contrast, off-site vegetation in the vicinity of *A. merriamii* populations was strongly dominated by *Atriplex confertifolia* (Table 5). This suggests that *A. merriamii* may occupy more saline habitats than does *A. californica.* From a physiognomic perspective, *Arctomecon* sites were dominated by perennial forbs, while off-site locations were dominated by shrubs and had much greater importance of perennial grasses than did on-site locations (Tables 4 and 5).

Percent Similarity (floristic similarity) between on- and off-site

TABLE 4. IMPORTANCE VALUES OF PERENNIAL SPECIES ON SITES OCCUPIED BY *ARCTOMECON CALIFORNICA* (ON) AND ADJACENT SITES WITHOUT *A. CALIFORNICA* (OFF) AT THREE LOCATIONS IN SOUTHERN NEVADA.

Species	Overton Beach		Stewart Point		Temple Bar	
	On	Off	On	Off	On	Off
Forbs						
Arctomecon californica	137	0	192	0	102	0
Baileya multiradiata	0	3	0	0	0	0
Enceliopsis argophyllum	0	0	0	0	0	16
Eriogonum inflatum	0	3	15	122	107	60
Lepidium fremontii	4	0	0	0	0	0
Psathyrotes ramosissima	0	0	0	5	0	0
Sphaeralcea ambigua	0	3	0	4	0	54
Stephanomeria pauciflora	4	0	37	24	0	0
Tiquilia latior	0	0	20	26	0	0
Tidestromia oblongifolia	0	0	34	0	0	0
Total	145	9	298	181	207	130
Grasses						
Erioneuron pulchellum	0	0	3	0	7	48
Hilaria rigida	0	73	0	0	0	0
Oryzopsis hymenoides	0	39	0	0	0	0
Total	0	112	3	0	7	48
Shrubs						
Ambrosia dumosa	52	113	0	49	0	24
Atriplex confertifolia	34	0	0	0	0	0
Ceratoides lanata	0	33	0	0	0	0
Ephedra torreyana	58	15	0	0	10	0
Hymenoclea salsola	0	0	0	0	31	0
Krameria parvifolia	0	3	0	0	0	0
Larrea tridentata	7	15	0	43	45	98
Psorothamnus fremontii	3	0	0	28	0	0
Total	154	179	0	120	86	122

locations for *A. californica* ranged from 20 to 37% for the three sites, and from 52 to 59% for two sampled sites for *A. merriamii*. At all sites sampled (3 for *A. californica*, 2 for *A. merriamii*), there were fewer species of vascular plants on-site than off-site. Vegetation similarity analysis showed that, for *A. californica*, the Coefficient of Community (CC) between paired on- and off-site locations ranged from 0.32 at Overton Beach to 0.50 at Temple Bar (Table 6). The on-site/off-site CC averaged 0.38 for *A. merriamii*. A comparison of on-site vegetation across sites resulted in CC's of 0.29 to 0.50 for *A. californica* sites and 0.80 for *A. merriamii* sites. A comparison of off-site vegetation across sites resulted in CC's of 0.42 to 0.57 for *A. californica* and only 0.18 for *A. merriamii*. Thus paired on- and off-site locations tend to have dissimilar vegetation

TABLE 5. IMPORTANCE VALUES OF PERENNIAL SPECIES ON SITES OCCUPIED BY *ARCTOMECON MERRIAMII* (ON) AND ON ADJACENT SITES WITHOUT *A. MERRIAMII* (OFF), AT TWO LOCATIONS IN ASH MEADOWS DESIGNATED AS SITES A AND B.

	Site A		Site B	
Species	On	Off	On	Off
Forbs				
Arctomecon merriamii	137	0	145	0
Enceliopsis nudicaulis	0	12	0	0
Lepidium fremontii	0	14	0	0
Psathyrotes ramosissima	0	15	0	0
Stephanomeria pauciflora	0	16	0	0
Tidestromia oblongifolia	0	12	0	0
Total	137	69	145	0
Grasses				
Erioneuron pulchellum	0	53	0	0
Total	0	53	0	0
Shrubs				
Allenrolfea occidentalis	0	0	0	61
Ambrosia dumosa	0	13	0	0
Atriplex confertifolia	163	166	155	171
Atriplex polycarpa	0	0	0	67
Total	163	179	155	299

and flora, similar to off-site locations that are significant distances apart.

Soil analyses for the three *A. californica* sites indicated that these sites had much higher levels of sulfur, calcium, and soluble salts, and much lower phosphorous contents, than did typical off-site locations that contain the dominant *Ambrosia-Larrea* vegetation type (Table 7). Total sulfur was over 10-fold higher on *A. californica* dominated sites than on adjacent off-site locations, total salts were

TABLE 6. COEFFICIENT OF COMMUNITY (CC) ANALYSES OF VEGETATION AT LOCATIONS WHERE *ARCTOMECON CALIFORNICA* OR *A. MERRIAMII* WAS PRESENT (ON) AND ADJACENT, NON-GYPSUM SITES WHERE *ARCTOMECON* WAS NOT PRESENT (OFF).

	Site comparison					
	On vs. off		On vs. on		Off vs. off	
Species	Site	CC	Sites	CC	Sites	CC
A. californica	OB	0.32	OB-SP	0.29	OB-SP	0.42
	SP	0.42	OB-TB	0.43	OB-TB	0.47
	TB	0.50	SP-TB	0.50	SP-TB	0.57
A. merriamii	A	0.36	A-B	0.80	A-B	0.18
	B	0.40				
Mean		0.40		0.51		0.41

TABLE 7. SOIL CHEMICAL PROPERTIES FOR THREE LOCATIONS AT THE OVERTON BEACH SITE: SITES WHERE *ARCTOMECON CALIFORNICA* POPULATIONS WERE PRESENT (ON); SITES WHERE *A. CALIFORNICA* WAS NOT PRESENT (OFF); AND ADJACENT SITES THAT APPEARED TO BE GYPSUM OUTCROPS BUT DID NOT HARBOR A POPULATION OF *A. CALIFORNICA* (SIM). N = 7 for each mean value.

Soil parameter	0–5 cm depth			6–15 cm depth		
	On	Off	Sim	On	Off	Sim
pH	7.8	8.5	8.0	7.9	8.6	8.0
Organic matter (%)	0.31	0.37	0.29	0.31	0.38	0.29
Soluble salts (ppm)	2.1	0.53	2.1	2.3	0.48	2.3
Total P (ppm)	1.1	9.3	2.9	1.4	3.2	1.9
$NaHCO_3$-P (ppm)	4.9	12.0	3.7	4.3	6.5	4.7
Ca (ppm)	5663	1660	5207	5687	1655	5189
S (ppm)	999+	75	999+	999+	10	999+
K (ppm)	151	115	151	162	108	225
Mg (ppm)	39.6	68.2	58.1	60.0	64.2	108
Na (ppm)	13.7	12.3	13.0	11.9	11.8	17.6
Zn (ppm)	0.51	0.60	0.66	0.53	0.53	0.64
Ca (% base saturation)	97.3	90.1	96.6	96.7	90.6	94.6
Mg (% base saturation)	1.1	6.1	1.7	1.7	5.8	2.0
K (% base saturation)	1.3	3.2	1.4	1.4	3.0	2.0
Na (% base saturation)	0.2	0.6	0.2	0.2	0.6	0.3

TABLE 8. SOIL CHEMICAL PROPERTIES FOR A SITE AT ASH MEADOWS WITH *ARCTOMECON MERRIAMII* AND AN ADJACENT OFF-SITE LOCATION WITHOUT THE SPECIES. N = 5 for each parameter at each depth and location.

Soil parameter	0–5 cm depth		6–15 cm depth	
	On-site	Off-site	On-site	Off-site
pH	8.8	8.8	9.1	8.8
Organic matter (%)	1.17	0.98	1.00	0.92
Soluble salts (ppm)	4.3	0.4	4.8	0.5
P (ppm)	1.6	1.2	1.8	1.0
$NaHCO_3$-P (ppm)	8.8	9.0	9.4	8.0
Ca (ppm)	1184	1430	1164	1424
K (ppm)	404	388	417	467
Mg (ppm)	87.6	150	70.2	146
Na (ppm)	1272	357	1554	377
S (ppm)	310	25	283	10
Zn (ppm)	0.34	0.44	0.30	0.44
Ca (% base saturation)	46.7	65.5	44.0	64.9
Na (% base saturation)	39.5	14.1	43.7	13.7
Mg (% base saturation)	5.8	11.3	4.5	10.9
K (% base saturation)	8.0	9.1	7.8	8.4

ca. 4-fold higher on-site, and total calcium was almost 3-fold higher than for off-site locations. In contrast, total phosphorous was ca. 9-fold higher off-site than on sites with *A. californica*; off-site soils were also consistently more basic (higher pH) than on-site soils. In order to correlate soil properties between sites, each soil parameter was relativized to a grand mean for that parameter across all three sites and both depths (Table 7) prior to calculating correlation coefficients. Using this method, on-site and off-site locations were found to be strongly negatively correlated ($r = -0.89$ and -0.88 at 0–5 and 6–15 cm depths, respectively; $P = 0.0001$ for each depth). Sites near *A. californica* populations that did not support populations of the plant but had visually similar soil surface morphology (i.e., they also appeared to be gypsum outcrops) were found to have soils that were significantly similar to soils which supported *A. californica* ($r = 0.84$ and 0.72 at 0–5 and 6–15 depths, respectively; $P = 0.001$ and 0.01 for the two depths).

Many of the trends in soils found on and off *A. californica* sites were also observed for *A. merriamii* sites, but there were some important differences. Large differences in the surface layer of the soil were found between on- and off-site locations for several soil components (Table 8). The percent base saturation of sodium, as well as total sulfur content, were greater on-site, while calcium, potassium, and magnesium were greater off-site. Differences in the lower layer of soil (6–15 cm) included total calcium and the percent base saturation of calcium and magnesium being higher where *A. merriamii* was present. Sites where *A. merriamii* was present were very different from off-site locations (r = −0.98 at both depths; P = 0.0001); surprisingly, off-site locations adjacent to *A. merriamii* populations, which are dominated by the halophyte shrub *Atriplex confertifolia*, were not higher in soluble salts than were off-site locations adjacent to *A. californica* populations. pH differences between sites with *A. merriamii* and off-site locations were negligible, but sites with *A. merriamii* populations had a subsurface pH of 9.1, versus a subsurface pH of only 7.9 for *A. californica* sites.

Discussion

Mortality of both species of *Arctomecon, A. californica* and *A. merriamii*, was highest during the early stages of the life cycle, a pattern that typifies most desert perennials. The greatest variation in mortality for *A. californica* was observed at the Stewart Point site, where mortality in each size class was above 10% and the largest size class exhibited 38% mortality (Fig. 1). The large number of adults in this population at the beginning of the study could have been a factor in the high mortality, as these individuals could have been near the age of natural senescence. Mortality in the largest size classes of *A. merriamii* (Fig. 1) may have been due to a similar cause, as all individuals originally mapped were size class 2 or larger (Table 1), with a few extremely large individuals (size class 6). The duration of this study was too short to sort out long-term trends in population demographics for these two species, but the size structure of the populations and the high seasonal variability in plant density (Table 2) suggest that *Arctomecon* population size may be primarily driven by episodic recruitment and mortality events.

Examination of reproductive potential from a phenological stage perspective revealed that the amount of reproductive attrition at the flowering stage was quite small for both species (Table 3). This may be attributed to the fact that the time spent in the flower stage is relatively short compared to that spent in the bud and capsule stages, which may be more vulnerable to abortion events simply due to their greater development time. Reproductive attrition was greatest at the bud stage for *A. californica*, although there was also a high loss at the capsule stage. Losses were primarily due to abortion of tissues at each stage, rather than to insect herbivory. A possible explanation for the high percentage loss in the bud stage may be due to the fact that many buds were initiated later in the flowering season, when abortion may have been higher as a result of water and/or high temperature stress. Many of these late buds aborted, whereas buds initiated earlier in the spring had lower abortion rates and were in the capsule stage by the time the late buds emerged. This fits the general trend of late-maturing buds being subject to higher abortion rates than are buds that emerge earlier in the flowering season (Stephenson 1981). High bud mortality can result in reduced inflorescence output, which may have a significant effect on total plant fitness. Pantone et al. (1995) found that inflorescence output was the most important reproductive attribute that resulted in reduced fitness of a rare taxon of *Amsinckia* and its widespread congener.

Although the percentage of buds lost was quite comparable across the three sites for *A. californica*, this was not the case for capsule abortion. Plants at Temple Bar showed a much smaller loss of capsules than did plants at Overton Beach and Stewart Point. This may have been due to fewer buds maturing to the capsule stage for Temple Bar plants, and thus fewer capsules to compete for limited resources from the plant on these nutrient-poor sites. Many of the capsules in each population of *A. californica* were well developed by mid-May, prior to the onset of hot, dry conditions in the summer months.

Arctomecon merriamii exhibited comparable abortion rates at the bud and capsule stages (Table 3), but these rates were much lower than for *A. californica*. This may be due to the fact that only a single bud occurs per stalk in *A. merriamii*, which may lead to higher resource supply and enhanced development per unit capsule in this species. However, it should be noted that the reproductive attrition rates in these two species of *Arctomecon* are low compared to long-lived Mojave Desert perennials such as *Larrea tridentata*, which has extremely high rates of bud, flower, and fruit abortion rates under natural conditions (Boyd and Brum 1983). It is thus noteworthy that these apparently high abortion rates cannot be implicated as a primary driving variable in the small, restricted status of *Arctomecon* populations in the region, although high bud abortion rates may result in significantly reduced total fitness in *A. californica*.

Compatibility experiments for *A. californica* showed a clear difference between the amount of seed set by buds on control plants and that set by buds unable to cross-pollinate by insect vectors; differences were also noted in the amount of seed aborted in control versus bagged buds. The Papaveraceae is thought to be a largely self-incompatible family (Faegri and van der Pijl 1979), which is supported by the results from *A. californica*. The fruit abortion data also supports the hypothesis that many fruits which are self-pollinated are more likely to abort than those which are cross-pollinated (Stephenson 1981). Compatibility experiments with *A. merriamii* did not yield as clear-cut results, however, with no significant differences observed between buds prevented from outcrossing and unbagged controls for either seed set or subsequent seed abortion. From these results it can be tentatively concluded that *A. merriamii* is able to self-pollinate when other individuals of the species are not nearby. This is logical and perhaps adaptive, considering the ecological isolation of the species. It has the widest geographical range of the three species of *Arctomecon*, but it is noted for occurring in scattered clumps with few individuals in each clump. The ability to self-pollinate would obviously be advantageous in such a situation. *A. californica,* on the other hand, occurs in scattered populations over a wide area, but those populations usually consist of hundreds of individuals, often in close proximity to each other. This would favor outcrossing within each population, although each allopatric population may be genetically distinct from other populations.

Vegetation of the sites where *A. californica* and *A. merriamii* are located are visually and quantitatively different from adjacent off-site locations where *Arctomecon* is not found. As first reported for *A. humilis* (Nelson and Harper 1991), *Arctomecon* populations occur in habitats where shrub cover is much less dense than for the landscape as a whole. Common shrub species of the Mojave Desert such as *Larrea tridentata*, *Ambrosia dumosa*, and *Ephedra* spp., if found at all with *Arctomecon*, are represented by greatly diminished numbers. Lowered species diversity and cover on *Arctomecon*-dominated sites leads to a more open environment. Results for *A. californica* sites showed that off-site locations had greater community similarity to distant off-site locations than to the *Arctomecon*-dominated sites nearby. For example, the Overton Beach on/off vegetation showed a 32% community similarity to each other, but when the Overton Beach off-site vegetation was compared with off-site vegetation near the Temple Bar *A. californica* population, a 47% similarity was seen despite the sites being ca. 40 km apart (Table 6). *A. merriamii* sites tended to be highly similar in vegetation structure, consisting of large numbers of *Atriplex confertifolia* and *A. merriamii,* whereas the off-site locations had higher plant diversity and differed in community composition relative to on-site locations, even though *Atriplex confertifolia* played a dominant or co-dominant role both on- and off-site. In this regard, *A. merriamii* appears to have more similar habitat requirements to *A. humilis* than to *A. californica*, given that *A. humilis* also tends to associate strongly with *Atriplex confertifolia* (Nelson and Harper 1991). However, *A. merriamii* is apparently not a gypsophile over its entire distributional range, whereas *A. californica* and *A. humilis* are (personal observations). Even so, when taken together these results indicate that the vegetation on *Arctomecon*-dominated sites is quite different from off-site vegetation, which remains somewhat similar over great distances in the Mojave Desert.

Quantitative analysis of soils on and off *Arctomecon*-dominated sites showed that sites which support *Arctomecon* populations have much higher total sulfur and soluble salt contents, and lower magnesium, than off-site locations (Tables 6, 7). High sulfur levels where *Arctomecon* was present, which are characteristic of gypsum-dominated soils, may have an effect on establishment of new plants, as sulfur content has been hypothesized to be an important factor in the establishment and success of certain species on gypsum soils (Parsons 1976). On sites which supported *A. californica*, soils contained lower phosphorous and magnesium levels and higher calcium and soluble salt levels than off-site (Table 6). Sites which supported *A. merriamii* populations showed much higher values of sodium and sulfur, and lower concentration of magnesium, than off-site locations (Table 7). Although these analyses point to strong differences in soil chemistry between *Arctomecon*-dominated and off-site locations, it has been proposed by Meyer (1986) that the important factor allowing some species to establish on gypsum soils but not others is due to surface effects of the soil, not to chemical factors per se. An important factor relative to the establishment of *Arctomecon* and other taxa on these soils may be the presence or absence of cryptogamic crusts. Many *Arctomecon*-dominated sites in southern Nevada, particularly sites with *A. californica*, can have an almost continuous cover of these surface crusts. Similarly, sites dominated by *A. humilis* in Utah exhibit a mean 84% cryptogamic crust cover (Nelson and Harper 1991). Cryptogamic crusts have been shown to increase nutrient levels in the top layer of soil (Harper and Pendleton 1993), which may be a factor in the success of *Arctomecon* on gypsum soils. They also strongly influence infiltration of rainfall, and thus influence surface water balance, and may also protect the often "fluffy" soils of gypsum outcrops from wind erosion.

Although a descriptive preliminary study such as this cannot conclusively determine what attributes of gypsum outcrops result in the apparent narrow edaphic requirements of *Arctomecon* to gypsum soils, it is clear that the imbalance in soil chemistry relative to off-site locations allows these plants to occur on sites where most other species apparently cannot become established. However, results for *A. merriamii* may be site specific, as this species has also been located on limestone outcrops, so its soil requirements may be more broad than for *A. californica* or its soil requirements may vary across its distribution. Further research needs to be conducted on the edaphic requirements of *A. merriamii,* as it is the most widely distributed of the three species of *Arctomecon,* but occurs in low density populations.

Soils were compared between sites that support *A. californica* and sites that did not support the species but appeared similar edaphically (i.e., were gypsum outcrops). Comparisons indicated that these two types of sites were highly correlated, and thus similar in soil structure and chemistry. Although this analysis may have failed to identify an important, but subtle, soil factor that limits the expansion of *A. californica* onto these sites, it does lead to the possibility that the local distribution of *A. californica* may not be based on soil requirements alone (indeed, sites in Utah that support populations of *A. humilis* show pronounced variability in several impcrtant soil parameters; Nelson and Harper 1991). A similarity in soils between occupied and closely adjacent non-occupied sites may also lead to the hypothesis that the establishment of *A. californica* on the non-occupied site has not yet taken place (i.e., the population could be expanding), but is a distinct possibility for the future. If so, these areas with no existing *Arctomecon* populations but with similar soils should be considered candidates for preservation as possible habitat that the species may utilize in the future. Alternatively, these sites with similar soils may have once supported *Arctomecon* populations, which have since contracted to more localized populations. This possibility would also argue for preservation of these sites with similar soils if the goal of management programs is to increase *Arctomecon* populations in the future, particularly if the proximate causes for contraction of *Arctomecon* populations are primarily related to anthropogenic disturbance.

Important management conclusions that can be drawn from this study include the observation that most of the mortality in *Arctomecon* populations occurs in the seedling stage, which is potentially important since the seedling stage is the precursor for future adult populations (Palmer 1987). Although almost all desert perennials exhibit highest mortality in the seedling stage, this becomes more important for the management of potentially endangered species such as *Arctomecon*. Since areas with many seedlings, for both *A. californica* and *A. merriamii*, will probably experience a high degree of mortality, it is essential that these populations be managed with care so that the few plants that survive to reproductive age can replenish the seed bank. Also, apparently not all habitat which is available is being utilized, as indicated by the soil analyses. Conservation of unoccupied, but similar, habitat is important for long-term conservation of the species, especially *A. californica*, whose habitat is continually encroached upon by urban development and ORV use. Since these edaphically-similar sites are usually adjacent to *Arctomecon* populations, protection of these sites would also provide needed buffer area for the existing populations.

In conclusion, high mortality of *Arctomecon* seedlings is considered a potential bottleneck in the preservation of both species. Reproductive attrition per se does not seem to be a critical factor in the survivorship of populations of either species. Isolation of *A. californica* plants could be highly detrimental to seed set, while such a situation does not appear detrimental to the more self-compatible *A. merriamii*. Preservation of unoccupied, but edaphically similar, habitat may be the best method of species preservation at this time. Currently, the relatively large geographical distribution of *A. merriamii* and its isolation from urban development leads to the conclusion that it is not in as great of a danger of extinction as is *A. californica*.

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